

A REVIEW OF DECOMPOSITION AND REDUCTION AND OF SOIL ORGANIC MATTER IN TROPICAL AFRICAN BIOMES

J. W. MORRIS

(Datametrical Services, Department of Agriculture, Private Bag X116, Pretoria 0001, R.S.A.)

ABSTRACT

Decomposition and reduction processes are described in relation to the chief causative organisms, namely, termites, ants, earthworms, dung beetles and micro-organisms while the effects of both inter- and intra-seasonal droughts on these processes and that of fire as a reducer agent are also discussed. Finally, a review of the humus status of tropical and subtropical soils, and non-forest ones in particular, is presented with particular reference to the possible reasons for the low soil organic matter contents generally found in such soils. It is concluded that further research in this field is required.

UITTREKSEL

'N OORSIG VAN DIE AFBRAAK EN REDUKSIE EN VAN GROND ORGANIESE INHOUD VAN TROPIESE BIOME IN AFRIKA

Afbraak en reduksie prosesse word beskryf in verhouding tot die hoof oorsaaklike organismes, naamlik, termiete, miere, erdwurms, miskruiers en mikro-organismes terwyl die invloed van beide inter- en intraseisoens-droogtes op hierdie prosesse sowel as vuur as 'n reduseerder ook beskryf word. Ten slotte, word die humusstatus van tropiese en sub-tropiese gronde, en nie-woud gedeeltes veral, aangebied met spesiale verwysing na die moontlike oorsake vir die lae grond organiese materiaalinhoud wat algemeen aangetref word in sulke gronde. Die gevolgtrekking word gemaak dat verdere navorsing in hierdie veld nodig is.

INTRODUCTION

In tropical and subtropical biomes, there are three possible fates for primary production that dies before being consumed by an animal. It may be consumed when dead (dead matter consumption and reduction), be decayed by micro-organisms (decomposition; also referred to as "oxidation") or be burnt. After a brief consideration of litter input, the processes of reduction and decomposition are dealt with in this review while herbivory (consumption) and fire are discussed to a much lesser extent. Dead organic matter plays a major rôle in determining the structure and function of an ecosystem by acting as a nutrient reservoir for intrasystem cycling and as an energy source for heterotrophic organisms (Singh & Gupta, 1977). Rates of decomposition and reduction and consequently the rate of nutrient release, eluci-

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dition of which is the usual reason for such studies, depend on the species concerned and abiotic factors of the environment as will be pointed out below. Aspects of the build-up of humus, an end-product of these processes, is an enigma in tropical and subtropical biomes and is therefore given prominence in a section of this review.

Species of termites, ants, earthworms, dung beetles, Coleopteran larvae, millipedes and cockroaches are the macrofaunal components identified as making the greatest contribution to dead matter breakdown and consumption to tropical and subtropical biomes. The relative importance of these groups varies from one biome type to another. Microbial activity is at least as important as the macrofaunal elements in the decomposition and reduction process and under tropical non-forest conditions has major differences in mode of functioning from both temperate and tropical forest ecosystems. Aspects of these differences are elaborated below. An outline of the processes involved in dead matter consumption and decomposition is also given.

In view of the paucity of data, a very wide definition of tropical and subtropical biomes is adopted although the geographical coverage of the review is heavily biased towards Africa. More emphasis is placed on botanical aspects than zoological although the subject is truly multidisciplinary, a reflection on the author's background.

LITTER DYNAMICS

In general modelling terms, inputs to the decomposition and reduction system are independent of the standing crop of dead organic material and outputs are proportional to, and therefore dependent on, the amount of the standing crop. The net rate of change in energy or material stored in an ecological system, or its parts, equals the rate of input minus the rate of loss (Olson, 1963). From one-year litter bag trials at the South African Savanna Ecosystem Project study site, Nylsvley, in the Northern Transvaal, Morris *et al.* (1982) reported the following half lives (time for the decomposition of half a given amount of litter) for freshly-fallen tree leaves: *Ochna pulchra* 5.5 years, *Burkea africana* 5.1 years and *Terminalia sericea* 2.9 years. Vegetative material of the two common grasses, *Eragrostis pallens* and *Digitaria eriantha*, both had half lives of 0.7 years. Values of k , the annual decomposition constant, for Nylsvley range from 1.20 for grass litter to 0.13 for *Ochna pulchra* leaves in litter bags. The decomposition constant for tree leaf litter at Nylsvley is between 0.13 and 0.33. Much faster rates are recorded by Malaisse *et al.* (1975): in miombo woodland, k varies from 1.11 to 1.32 (the latter in the presence of fire) and k is 1.40 in dry evergreen forest. Rates from 2.0 to 4.85 are quoted for mixed dry lowland forest. In Senegal, Bille

(1978) records values for the monthly rate of disappearance of dead matter ranging from 0.37 to 0.64 (at the end of the rainy season) to 0.09 to 0.15 (during the dry season). Where an annual burn is part of the environment, such as at Lamto (Côte d'Ivoire) such calculations are not appropriate and values are not available. Ashton (1975) records half lives of 0.82 and 1.98 for leaf and total litter, respectively, from *Eucalyptus regnans* forest near Melbourne, Australia.

PROCESSES

Generalisations about dead matter consumption and decomposition processes in tropical and subtropical biomes are difficult to make as the range of patterns within such biome types is almost as great as the range between them. The best data available on these patterns are from Lamto, a moist, rather atypical "savanna"¹ adjacent to tropical rainforest (Lamotte, 1977 and 1978; Anon, 1979a). At Lamto, dead matter consumption and decomposition are largely due to the activities of termites, earthworms and microarthropods (Lamotte, 1975 and 1979). Ants are also involved, as well as myriapods and the underground larvae of Coleoptera. It seems that drier biomes, as exemplified by Nylsvley, show a markedly different pattern with reducers being more important relative to decomposers, termites of great importance and earthworms unimportant (Morris *et al.*, 1982; Huntley & Morris, 1982). At Lamto, animals account for nearly 15% of the mineralisation of organic matter while the mechanical action of these populations (soil movement and organic matter transformation) seem even more important than mineralisation (Anon, 1979a). The individual rôles of important agents are discussed below.

Of the key ecological processes operating in tropical and subtropical biomes, the inter-seasonal soil moisture deficit and fire have certain, probably rather minor, influences on dead matter consumption and decomposition, making these processes rather different from those in other biomes. In all but the most moist of such biomes, the intra-seasonal intermittent desiccation of litter in the wet season, on the other hand, may have considerable ramifications on the processes.

Termites

Termites are inhabitants of tropical, subtropical, semi-arid and, to some extent, warm temperate regions (Allison, 1973; Wood, 1976). The vast ma-

¹ On the advice of a referee, the term "savanna" has been avoided except where used in quoted literature as the term in the African context was unanimously recommended as being unacceptable to botanists and ecologists as long ago as 1966 and the resolution has been endorsed by many scientists down ensuing years.

jority of research on decomposition processes has, however, been done in cool temperate regions (Anderson & Macfadyen, 1976) and although a few species of termites occur in these regions they have little impact on decomposition processes. Where termites are abundant, their activities are sufficient to generate new pathways of decomposition, in comparison with temperate regions (Wood, 1976). According to Russell (1961), termites in tropical soils seem to be the predominant animals affecting the soil and the plant. The rôle of humus-feeding species in pedogenesis is to produce, through their faeces, a more stable organic matter substrate for the physiochemical and bacterial agents of degradation (Malaisse *et al.*, 1975).

On the basis of diet, there are three kinds of soil-inhabiting termites: wood feeders, fungus growers and humus feeders (Harris, 1955). At Lamto, foraging, humivore and fungus-growing termites are the three main groups (Lamotte, 1975). Harvester termites are an important ecological group which feed on living and dead grass while other termites either forage for or live in dead wood, or even living trees. Species differ greatly in their diet, specificity and habitats and most typical non-forest biome sites have a diverse termite fauna. At least 20 species, for example, have been identified at Nylsvley (Ferrar, 1982a & 1982b) and 36 species are recorded from Lamto (Wood & Sands, 1978).

The food of termites consists of plant material of all kinds, including wood, grasses, herbs and roots, in the range from living plants to decomposed plant remains mixed in mineral soil. Soil-feeding has been adopted as a specialised habit by many species of higher termites. In tropical non-forest regions, where levels of organic matter are notoriously low (Wood, 1976), termites may be partly responsible for reducing organic matter content. Cellulose is the main carbohydrate utilised by termites that feed on wood or vegetable matter. Digestion in most species is brought about by flagellates or bacteria that live in the intestines and secrete cellulase. The five families of lower termites (about 25% of known species) have flagellates while the higher termites (Termitidae) have no flagellates but do have bacteria (P. Ferrar, pers. comm.) The species that do utilise organic residues do so very completely and markedly hasten the decomposition process (Allison, 1973).

There are many common termite species which move large quantities of soil, sometimes ingesting much of what they move, bringing grass and other plant material into the soil and burrowing and tunnelling through the soil in the process (Russell, 1961). Unlike other soil animals which deposit faeces within the soil where they are available to micro-organisms and coprophagous invertebrates, termites use their excreta to construct certain regions of the nest or to construct fungus combs which are further utilised as food (Wood & Sands, 1978). Thus organic material and the nutrients it contains are collected from a wide area and concentrated largely in the central region

of the nest system. Through the concentration of nutrients in nests, termites contribute to the patchiness of nutrient distribution in soils. This process has an impact on the vegetation, resulting in greater species diversity and stronger patterns (Malaisse, 1978). Trapnell *et al.* (1976) report the lack of significant change in nitrogen and carbon in soils under various fire regimes in Zambia. After 23 years without burning the organic matter content had not changed appreciably. At the same time they report that termite mound material had over three times the organic carbon content of adjacent surface soil. A proportionally still greater increase in exchangeable bases is reported. Wood- and litter-consuming species are considered responsible for the limitation of humus sources under fire protection. Lee & Wood (1971) and Wood & Sands (1978) also report that some termite mounds have concentrations of organic matter higher than the soil from which they are constructed.

The distinction has, however, to be made here between the humus-feeding species which build mounds with an excreted paste and the wood- and litter-feeding large-mound builders which construct their foraging passages and spires with soil particles carried up from subsoil far below the surface and bound by salivary matter (Trapnell *et al.*, 1976). Analyses of mound material with organic matter and nutrient contents lower than adjacent top soil but closely similar to the subsoil are summarised by Wood & Sands (1978). Subsoil is brought to the surface from a depth of from one to more than three metres (Allison, 1973). The large mounds that may reach a height of 10 metres provide microclimates and shelters for a wide range of plants and animals within the "savanna" matrix (Malaisse & Anastassiou-Soquet, 1977).

Ants

In South America, ants replace termites in some of the scavenging and reduction rôles that the latter occupy in Africa. Data are available from Surinam, Brazil and other tropical South American countries. It is reported by Bucher (1982) that ants are of considerable importance in the Chaco as a result of their great abundance and degree of ecological diversification. Some species of leaf-cutting ants are specialised as detritus feeders, particularly taking fallen leaves and insect frass. They are extremely abundant in the Chaco dry woodlands and as they carry litter underground for fungus-growing, they also have an important rôle in nutrient cycling and redistribution. Ants are a relatively minor contributor to soil formation and organic matter decomposition according to Allison (1973). He considers that their chief rôle in soil formation lies in the transport of subsoil to the surface.

The rôle of ants in ecosystems is reviewed by Petal (1978). Rôles similar to those described above for termites are reported although they appear to occupy a wider range of niches than termites. Accumulation of nutrients and

organic matter in nests as well as the opposite effect are found (Petal, 1978). Description of the important rôle of ants as consumers is beyond the scope of this review.

Earthworms

Earthworms are intolerant of drought and frost and hence dry sandy soils and thin soils overlying rock are not usually favourable environments for them (Anon, 1979a). They also need reasonably aerated soil and can only flourish in soils well provided with organic matter (Russell, 1961). As conditions in drier tropical and subtropical biomes are not often suitable for earthworms, it is not surprising that they are seldom common except in moist habitats, such as found at Lamto, where soil organic matter content is low (J. C. Menaut, pers. comm.). Some soil-dwelling termites appear, in fact, to be the tropical analogue of the earthworm (Russell, 1961).

Dung beetles

The main group of dung beetles involved with the reduction of dung is the Scarabaeinae (Coleoptera), which are only active in fresh dung. The attack on dried dung by termites appears to be a characteristic feature of tropical and subtropical non-forest biomes, judging from evidence from South America, Lamto and Nylsvley. Dung beetles attack dung in three main patterns, of which the best known is perhaps by beetles fashioning lumps of fresh dung into spherical balls and rolling them away some distance for burial (Bornemissza, 1979). More common, but less well-known, are those which bury fresh dung on the spot by digging tunnels which may end in chambers. The third, and insignificant group, excavate old dung pads.

The lack of an indigenous Coprophagous fauna in the Australian hinterland for the efficient treatment of cattle dung is worth noting. Although there are 250 species of dung beetle in Australia, very few find the soft cow pads with their high water content attractive (Bornemissza, 1979). The problems arising from dung pollution in the absence of these organisms in Australia is a good example of the essential rôle decomposers and reducers have in a system, whether natural or artificial.

Micro-organisms

The complex relationships between groups of micro-organisms and specific environmental factors under tropical conditions are reviewed by Mohr *et al.* (1972). Moisture, access of air, temperature, acidity and the supply of food materials have different but rather marked influences on the number of micro-organisms as well as their activity. Generally, conditions appear to favour bacteria in the lower warmer tropics while fungi predominate in cooler climates found at higher altitudes.

Fire

In non-forest tropical and subtropical biomes, fire is an important, if not the most important, agent of dead matter "respiration", in comparison with its minor influences on consumption and decomposition. The subject of fire in these biomes is beyond the scope of this review and only some aspects directly related to decomposition and reduction will be mentioned.

The major effect of fire is the removal of living material (which is potential input to the dead organic matter compartment), standing dead plant parts and litter and the associated release of organically bound mineral elements in the form of ash. Fire will also kill a proportion of the organisms in the remaining litter and will make post-fire soil and litter temperatures more extreme. Blackened surfaces will absorb more heat while reduced shading of the surface by plants and litter will result in raised maximum day-time and lowered minimum night-time temperatures. Decomposer organisms can be expected to recover from fire fairly quickly while reducers, through a decrease in the quantity and quality of their food source, will recover more slowly.

If fire is excluded from a vegetation type in which fire is normally a major reducer, there will be a build-up of dead organic material until the steady state standing crop is reached. The steady state is approached asymptotically and the final amount may be considerable. Such a system has relevance to the frequency of fire in that a vegetation prone to fire will have a high primary production and either a low herbivory rate or a low dead matter consumption and decomposition rate, or both.

EFFECTS OF SOIL DROUGHT

Inter-seasonal drying

Inter-seasonal drying is likely to have effects that are either too broad or too subtle to be easily identified. In wetter biomes, organisms such as earthworms are able to survive such drying whereas in drier biomes, dry periods within the wet season (see below) will have marked effects confounding the effects of the dry season. Micro-organisms are unlikely to be inhibited during the wet season by the necessity to survive the dry season in spore form. There may, however, be certain effects on the timing of nutrient release attributable to drying out of litter, possibly enhancing leaching at the beginning of the subsequent wet season.

Intra-seasonal drying

Considerable effects may result from the frequent dry periods during the wet season, during which litter dries out to a great extent. This is a major

contributory factor to the slow decomposition rate recorded for non-forest tropical biomes. Micro-organisms are not only inactive in dry litter but have to build up in numbers when the litter is re-moistened. This pulse activity may itself influence the micro-organism species present as they will usually be present in small numbers within the litter and will therefore rarely be competing with each other. The wetting-drying cycle within a season may have appreciable effects on nutrient release not observed in a continuously-moist litter. If nutrients, and especially nitrogen, are more easily washed out of dead micro-organisms than from living ones or dead plant matter, then there would be a pulse of nitrogen leached at the start of each rainy period and rain season.

The slow rate of decomposition in drier tropical and subtropical biomes is likely to have a large number of effects on dead matter consumption and decomposers. Just as secondary production in different biomes has been characterised as reducer- or consumer-dominated, dead matter consumption and decomposition in drier biomes is reducer-dominated with a relatively minor rôle played by decomposers. The opposite holds in moist biomes, resulting there in low standing crops of litter. In drier biomes, reducer organisms, with superior water conservation relative to micro-organisms, are able to survive dry periods and play an important rôle in dead matter consumption and decomposition. Termites have a particularly effective water conservation system. In moister ecosystems, the termite moisture control system (tunnels built for foraging) becomes a handicap as it requires considerable energy to maintain. Other, more mobile reducers, take over and decomposers will be better able to decay material.

SOIL HUMUS STATUS

The relatively slow decomposition rate noted for dry tropical and subtropical biomes makes it difficult to explain the documented absence of a well-defined humus layer in the soils of drier biomes (Anon, 1978; Greenland & Nye, 1959; Vine, 1968). In moist biomes including tropical and subtropical forest, high soil and litter moisture contents and high temperatures result in the rapid breakdown of dead organic material and the formation of a distinct humus layer. In drier biomes, one or both of these two factors may be inoperative while, of course, primary productivity and thus input to the litter compartment are also lower. Although the breakup of litter is rather slow, once it has broken up and is in small fragments, either on the soil surface or mixed into the topmost soil layer, the moisture conditions of the material become much more favourable for rapid decomposition. Fresher material on top of small fragments protects the latter from desiccation to a certain degree and soil will usually have far better moisture retaining pro-

perties than litter so that once the fragments have become incorporated into the soil, decomposition is facilitated. The process is further accelerated by high temperatures relative to temperate region ecosystems. It is also suggested that leaching and runoff following tropical downpours could account for the absence of a humus layer. Light humus particles on the soil surface could also be blown away by wind erosion. Some apparent contradictions and gaps in our knowledge with regard to soil humus status became apparent during the writing of this review, these being presented below with the intention that they spur further research. Both Anon (1979a) and Rodin & Bazilevich (1967) stress that very little research has been undertaken to date in this important field, with particular reference to tropical and subtropical areas.

Soil humus is of great importance in the soil-formation process and in soil fertility maintenance (Anon, 1979b). Mohr *et al.* (1972) consider soil organic matter to be the dominant factor in soil formation. As well as being a valuable source of nutrients, particularly nitrogen, the organic matter in tropical and subtropical biome soils is important in maintaining their structure, water-holding capacity and resistance to erosion and in providing much of their cation exchange capacity (Jones, 1973). Organic matter influences physical and chemical properties of soils far out of proportion to the small quantities present, accounting, for example, for at least half their cation exchange capacity (Brady, 1974). Within the tropics, soil organic matter has been shown to increase with increasing altitude, increasing rainfall and decreasing temperature (Jones, 1973). Nye & Greenland (1960) note that in tropical soils, decreasing rainfall is correlated with lower organic matter content. The optimal conditions for mineralisation of plant residues are found where temperatures are high and soil moisture satisfactory, such as in the low hilly regions of the tropics, and consequently little organic matter will remain in its original or humified state (Mohr *et al.*, 1972). On the other hand, at higher elevations organic matter will accumulate; the higher the elevation the more humus remains (Mohr *et al.*, 1972).

The formation of humic substances is due to complex transformations of the original organic residues and the process and products are described as follows by Kononova (1961). In forming humus, the enzymatic activity of both micro-organisms and macrofaunal elements are important. A first group of substances in soil humus, derived from decomposing plant and animal residues and being products of their decomposition and re-synthesis in micro-organisms, consists of various nitrogenous and non-nitrogenous organic compounds belonging to well-known groups of organic chemical compounds such as proteins, carbohydrates, organic acids, fats, waxes and resins. A second and larger fraction consists of humic substances. Because of the peculiarity of their nature they cannot be related to any existing

groups of organic chemical compounds. Their nature, origin and properties are not yet fully understood. Schnitzer & Khan (1972) state that the mode of formation of humic substances has been the subject of much speculation and list four hypotheses which have been proposed for their synthesis. They conclude that it is difficult to state which of the four hypotheses (plant alteration, chemical polymerisation, cell autolysis and microbial synthesis) is the more valid one.

Greenland & Nye (1959) have found that decomposition constants for lowland (tropical) forest soils are about three times larger than those of non-forest tropical biome soils. They consider that the low rate of decomposition in the latter soils is probably connected with the repressive effect which grasses exert on humus mineralisation, as shown by the very low levels of nitrate in such soils. For comparison, constants for temperate-zone oak and pine forests have humus-carbon decomposition constants closely similar to those for highland tropical forests. The loss of organic matter caused by high rates of respiration at high soil temperatures is not always the primary cause of low organic matter contents in tropical soils (Greenland & Nye, 1959). The effects of low returns of organic matter due to burning and soil erosion are also very important in their estimation. Nye & Greenland (1960) note that burning in tropical biomes reduces the buildup of humus in the topsoil by reducing the amount of litter supplied to the soil organisms. The organic matter content of the surface horizons of non-forest soils is considerably lower than that of forest soils because of the reduced additions of organic matter from the vegetation. The exchange capacity is consequently lower (Nye & Greenland, 1960).

Greenland & Nye (1959) have pointed out that in the tropics the relationship between soil organic matter and vegetation type is the reverse of what is found in the temperate zone (see also Jenny, 1950; Greenland & Kowal, 1960; Sanchez, 1976). In the tropics, much the largest addition of organic matter to the soil takes place under forest vegetation and the soil organic levels tend to be greater than under non-forest vegetation types. In the temperate zone, on the other hand, soil organic matter production tends to be greater on grassland areas and it is the grassland soils which have the highest levels of soil organic matter. A factor seldom considered in such general comparisons is that input from primary production should include both above- and below-ground plant components, where the latter are very difficult to quantify.

The organic matter content of certain tropical soils, especially the forested ones, is low, according to Allison (1973), primarily because of the high temperatures and rainfall, abundant plant and animal life in the soil and the scarcity of inorganic colloids with which the organic matter might combine. Tropical soils can nevertheless support large amounts of vegetation per unit

area because moisture and temperature are suitable for growth while roots bring up nutrients from the subsoil and also intercept nutrients that are being carried down by rainwater.

Allison (1973) also states that organic matter decomposes at a slower rate in the presence of clay than in sand. According to Sanchez (1976), in general, the higher the clay contents, the lower will be the annual decomposition rate of soil organic carbon. This finding is supported by Jones (1973) who also notes that, in general, amounts of organic matter and nitrogen in the surface soils of the West African "savanna" are small. The mean carbon content of 605 well-drained sites was 0.68%. Two important factors governing amounts of organic matter in well-drained soils appear to be the clay content and a moisture factor related to the length of the wet season (Jones, 1973). Multiple linear regression on soil clay content and rainfall accounted for 46.5% and 57.2%, respectively, of the observed variability of soil carbon and nitrogen contents. These findings suggest that the low levels of organic matter in "savanna" soils arise from their predominantly sandy nature and from the relatively low rainfall.

Jones (1973) states that soil organic matter status is undoubtedly closely related to the rate of return of organic residues to the soil and, hence, the type of vegetation. Both vegetative growth and soil microbiological activity are closely controlled by soil moisture. He suggests, therefore, that the length of the rainy season is more important in determining organic matter status than annual rainfall and notes that the essential factor embracing both rainfall and drainage factors is the annual period during which the soil is moist, but unfortunately, such information is rarely available.

The amount of organic material in a soil is the product of a number of diverse factors (Jones, 1973) acting over a period of time on the relative rates of the return of organic residues to the soil and their subsequent breakdown in the soil. In "savanna", Jones considers, it is probably the effective length of the wet season that is more important in determining soil organic matter levels than annual rainfall. Birch & Friend (1956) recognised one major factor, namely rainfall, as having an overall influence on soil organic matter status in East African soils and two minor factors, temperature and clay content, that exercise a modifying influence.

CONCLUSION

In writing this review, some speculation has been included because of a lack of sufficient data relevant to tropical conditions. It is hoped that this paper will, to some degree, provide an impetus for further work. There is obviously a great need for comparative data on the fates of primary production in tropical and subtropical biomes of various types, including detail within the dead matter consumption and decomposition components. Fur-

ther study of soil organic matter levels would also appear to be appropriate as conflicting accounts abound in the literature.

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